# A NEW CLASSIFICATION OF THE ORDER PERLARIA.

BY R. J. TILLYARD, M. A.
Sc. D. (Cantab.) D. Sc. (Sydney), F. L. S., F. E. S., Chief of the Biological Department, Cawthron Institute of Scientific Research, Nelson, New Zealand.

For some years past I have been studying the Perlaria of Australia and New Zealand, about which little has been made known up to the present. Taken in connection with the forms already described from Southern Chile, Patagonia, Tierra del Fuego and the Subantartic Islands, these insects form a very distinct Notogæan Fauna, clearly marked off from the Perlaria of the Northern Hemisphere and of the Tropics by the fact that it is made up almost entirely of very archaic types. No representatives of the highly specialized Perlidæ (including Perlodidæ) occur in these regions; no Pteronarcidæ, in the strict sense in which that family will be defined in this paper; no Capniidæ, Taeniopterygidæ or Leuctridæ; and only one or two isolated forms of Nemouridæ (genus *Udamocercia* of Enderlein).

In attempting to classify the known Notogæan forms of Perlaria, I have had recourse not only to all available imaginal characters, but also to as careful a study of the individual life-histories as the rareness of most of the forms would permit. I am now able to state that, as regards Australian and New Zealand forms, the classification adopted by me, on imaginal characters only, has been fully tested in the case of the corresponding larvæ, with the result that these latter are found to group themselves into distinct families as readily as do the imagines, so that the two sets of characters taken together form a most useful and easily understood classification.

The most archaic forms of Perlaria extant are to be found in the genus *Eusthenia* and its allies. These have no close relationship with the Pteronarcidæ as defined in this paper, the latter being specialized by the reduction of the mandibles, the approximation of the coxæ of the forelegs, by the loss of the primitive paired abdominal appendages on segments 1–6, (secondary gill-tufts on the thorax and base of abdomen are developed in some genera), as well as by loss of the original palaeodictyopterous mesh-work or *archedictyon* in the anal area of the hindwing, and by the presence of a distinct break in the contour of the outer margin of the hindwing, at the distal end of $Cu_2$, where the anal fan leaves the rest of the wing. Thus the only primitive characters left to the Pteronarcidæ in common with the Eustheniidæ proper are the form of the tarsal joints, the visible clypeus and labrum and the presence of numerous cross-veins in the distal portions of the forewing. In contrast with this, all the true Eustheniidæ have a primitive larval form possessing five or six pairs of lateral abdominal appendages functioning as gills, on the first five or six segments of the abdomen, but no secondary gill-tufts at all. These primitive paired gills are closely similar to those found in the larvæ of certain archaic Calopterygidæ in the Order Odonata. They are carried over into the imago at metamorphosis, as are the secondary gill-tufts of *Pteronarcys*, but quickly shrivel up. In the imaginal stage, true Eustheniidæ possess an altogether complete set of archaic characters, as follows: In the forewing, a complete archedictyon or cross-venation in all parts of the wing, a complete set of cross-veins between $Cu_2$ and 1A, a radial sector with three or more branches, a first

cubitus with two or more branches, in most genera showing a primitive anteriorly-arching type of branching, and at least three complete anal veins; in the hindwing, the outer margin with a single complete convex contour, without any re-entrant break or angle at the distal end of $Cu_2$ (this character is unique for

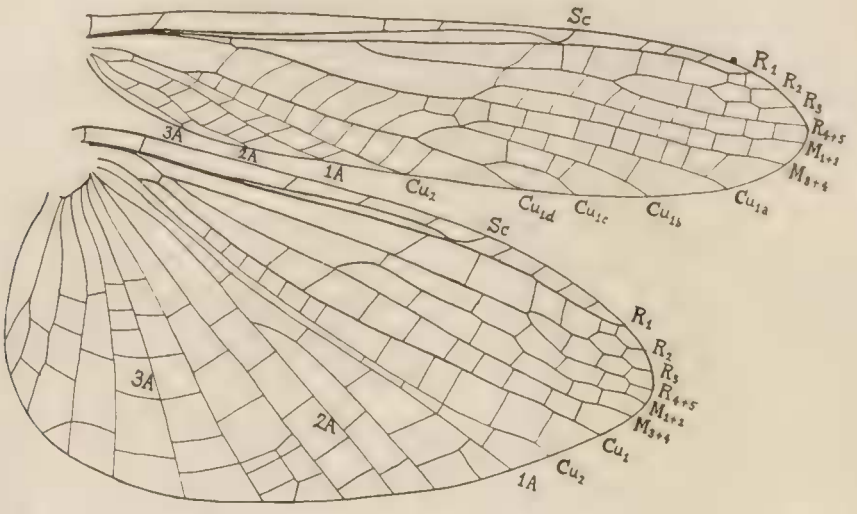


*Fig. 1.*—Venation of *Stenoperla prasina* (Newm.), family Eustheniidae, (New Zealand). The genus *Eusthenia* itself has broader wings and still denser venation.

the family), the radial sector branched, and the archedictyon completely preserved on the anal fan, as well as on the rest of the wing. (Text Fig. 1*). Other archaic characters are the form of the tarsal joints, the wide separation of the front coxæ, the presence of strong functional mandibles and a clearly visible clypeus and labrum.

Separated from these by clear characters, but still very archaic, are the genera *Austroperla* Needham and *Tasmanoperla* n. g. (type *Eusthenia diversipes*, n. sp.), which differ from the true Eustheniidæ in having shorter cerci, somewhat more reduced but still primitive venation, at least a partial fusion of $M_{3+4}$ with $Cu_{1a}$ in the hindwing, no archedictyon on the anal fan, and a distinct re-entrant angle on the outer margin at the distal end of $Cu_2$. (Text Fig. 3). In order to test the validity of this family, I sought carefully for larvæ of a different type from those of Eustheniidæ, and finally discovered in Tasmania a long cylindrical larva without any gills at all, and with rather short cerci, from which I reared a new species of *Tasmanoperla*, not yet described. Later on, I also obtained a closely similar type of larva from New Zealand, and reared from it *Austroperla cyrene* Newm. Thus the formation of this new family was fully justified.

Numerous species occur in which a considerable measure of specialization has set in, coupled with the retention of a number of archaic characters. These are all closely related to the genera *Leptoperla* of Newman (1839) and *Gripopteryx* of Pictet (1841). They therefore form the family Leptoperlidæ, this name replacing the name Gripopterygidæ used by Enderlein to include not only these insects, but also the Eustheniidæ and Austroperlidæ of this paper. Parenthetically, it may be remarked that Enderlein, in forming his family, entirely ignored

*An excellent figure of the wings of *Eusthenia spectabilis* Gray is to be seen in Comstock's "The Wings of Insects," (1918), p. 247, Fig. 246.

Newman's genus, and did not even give it a place in his dichotomic tables, though he must have known of its existence.

The characters that distinguish the Leptoperlidæ, as here defined, (Text. Fig. 4), are the loss of 1A in the forewing, leaving only two anal veins, 2A and 3A, of which the latter is always forked; the cubitus of the forewing either simple or once forked; the absence of archedictyon in the anal area of the hindwing; the presence of the re-entrant angle at the distal end of $Cu_2$; the presence in the hindwing of a fusion of $M_{3+4}$ with $Cu_1$ for part at least of their lengths; the possession, as in Eustheniidæ and Austroperlidæ, of the archaic type of tarsal joints, mandibles, clypeus and labrum, and the widely separated front coxæ. In the larvæ, there is a unique development of a rosette of gill-filaments around the anus; no other type of gill is present.

There remain over only a few very reduced forms of Nemouridæ, found equally in Australia, Tasmania, New Zealand and Southern Chile, of which the genus *Udamocercia* End. contains at present the only described species. These are true Nemourids in the widest sense, the imagines having the cerci reduced to one joint, while the same is true for the larvæ, which also have no visible gills.

Owing to a fortunate meeting with Mr. Nathan Banks, of the Museum of Comparative Zoology at Cambridge, Mass., I have recently been able to discuss my plan of classification for the Notogæan Perlaria with him, and to learn from him more details of the morphology of those genera not represented in our Southern fauna than was possible with the limited material at my command. I wish here to express to Mr. Banks my very grateful thanks for a very illuminating discussion which I had with him, in which he clearly set forth the main characters of the various genera of the Northern Hemisphere, and pointed out what he considered the basic errors of accepted classifications. As soon as I had succeeded in convincing him that the Eustheniidæ and Austroperlidæ, as defined in this paper, had no close relationship with the Pteronarcidæ proper, the rest became "plain sailing," and we soon arrived at a complete scheme of classification which illustrates the phylogeny of the Order well, and at the same time offers excellent characters for the systematist.

The first point to be noted is that the old line of evolution which began with the Eustheniidæ and Austroperlidæ, is carried on by the Nemouridæ and Capniidæ. Both these families retain the original form of mandibles, clypeus and frons, while they also keep the primitive widely separated front coxæ. As regards their wing venation, both can be developed by further specialization from types found within the Leptoperlidæ; but the Capniidæ have progressed a point further than the Nemouridæ, in having lost the fork of 3A in the forewing. On the other hand, the Capniidæ have retained the original many-jointed cerci; while, in the Nemouridæ, these processes are reduced, both in larva and imago, to a single joint. Mr. Banks and I quite agreed that the elevation of the groups of *Taeniopteryx*, *Nemoura* and *Leuctra* to full family rank was not justified; and, in this paper, these groups are considered to be only subfamilies of the Nemouridæ.

The second point to note is that the two families Pteronarcidæ and Perlidæ (this latter including the Perlodidæ, which are at most only a subfamily of the Perlidæ) form an evolutionary sideline marked by certain high specializations

coupled with a primitive venational scheme, viz., reduction of the mandibles to a weak lamina, (in the case of *Perlidæ* followed by an inturning of the clypeus and labrum under the frontal shelf, so that neither of these parts is visible from above), and, in the larva, either absence of gills or replacement of the original segmental gill-appendages of the abdomen by secondary gill-tufts around the bases of the legs and on the first two abdominal segments. Within this complex, the Pteronarcidæ keep the more primitive form of venation, very similar to that of the Austroperlidæ; like these latter, they have lost both the archedictyon of the anal fan and also the original complete contour of the outer margin of the hindwing. They are also specialized in a unique manner by the approximation of the fore coxæ. On the other hand, the Perlidæ have a somewhat more advanced venational scheme, though some of the original cross-venation still persists in the Perlodinæ; the fore coxæ remain widely separated, but the joints of the tarsi become specialized, both first and second joints being very short, and the third much longer than both these two together. The Perlodinæ differ only from the Perlinæ in the more complete cross-venation of the distal portion of the wing, and therefore cannot be granted at the most more than subfamily rank.

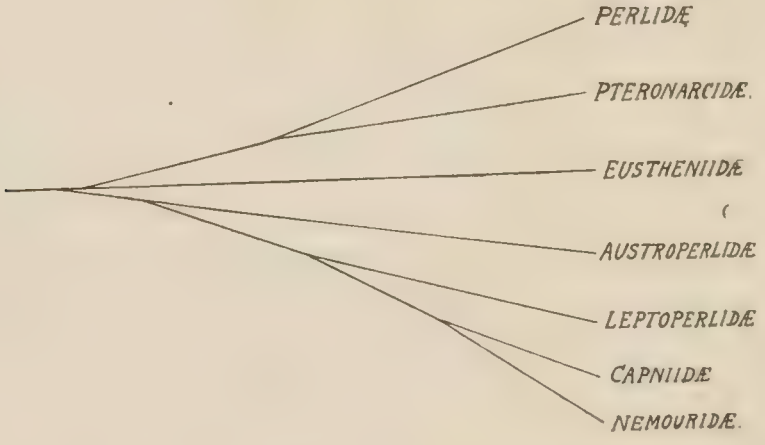


*Fig. 2.*—Phylogenetic diagram to show the relationships of the various families of the Order Perlaria. The Eustheniidæ are the remains of the original stock, without any specialized characters. The main line of evolution leads first to the Austroperlidæ, from them to the Leptoperlidæ, and culminates in the Capniidæ and Nemouridæ. From far back along the Eustheniid line, an evolutionary sidebranch gave origin to another distinct group, out of which arose the Pteronarcidæ and the Perlidæ.

The differences of the various families may be clearly set out in the following table, in which characters marked A are to be regarded as archaic, those marked B as specialized, while the addition of the letter U to either indicates that it is unique for the family. In the last line, the percentage of archaic characters present for the most archaic members of each family is calculated, the number so obtained giving a fairly reliable indication of the position of the family in the line of evolution. It should always be borne in mind that there are two culminating points for the family, viz., the Perlidæ on the one hand, as the end of a side-branch of evolutionary effort, and the Nemouridæ on the other, as the end of the main line of ascent of the Order. This idea is indicated in the Phylogenetic Diagram given in Text Fig. 2.

## Table Showing Principal Characters For The Families of The Order Perlaria.

| Character | Family | | | | | | |
|---|---|---|---|---|---|---|---|
| | *Eustheniidæ* | *Austroperlidæ* | *Pteronarcidæ* | *Perlidæ* | *Leptoperlidæ* | *Capniidæ* | *Nemouridæ* |
| (1) Mandibles:—A normal; B, reduced to lamina.... | A | A | B | B | A | A | A |
| (2) Clypeus and Labrum:—A, normal; B, hidden.... | A | A | A | BU | A | A | A |
| (3) Palpi:—A, with short joints; B, one or more joints elongated..... | A | A | A | B* | A | B* | B* |
| (4) Anterior coxæ:—A, wide apart; B, approximated. | A | A | BU | A | A | A | A |
| (5) Tarsal joints: — A, 2 least, 3 longer than 1; B, otherwise ..... | A | A | A | B† | A | B† | B† |
| (6) Cerci:—A, with 5 or more joints; B, reduced to a single joint..... | A | A | A | A | A | A | BU |
| (7) Outer margin of hindwing:—A, complete convex whole; B, with reentrant angle at distal end of $Cu_2$ ..... | AU | B | B | B | B | B | B |
| (8) Anal fan:—A, with cross-veins; B without.. | AU | B | B | B | B | B | B |
| (9) Cross-veins in distal half of forewing: — A, present; B, absent..... | A | A | A | A(B) | A | B | B |
| (10) Cubito-anal cross-veins in forewing: — A, present; B, absent..... | AU | B | B | B | B | B | B |
| (11) Branches of Rs in forewing:—A, 3 or more; B, 2 or 1..... | A | A | A | A(B) | B | B | B |
| (12) Branches of $Cu_1$ in forewing:—A, 3 or more; B, 2 or 1..... | A(B) | A(B) | A | A(B) | B | B | B |
| (13) Anastomosis or transverse cord:—A, absent; B, present..... | A | A | A | A(B) | A | B | B |
| (14) 1A in forewing: — A, present; B, absent..... | A | A | A(B) | B | B | B | B |
| (15) 3A in forewing: — A, forked; B, simple..... | A(B) | A | A | A(B) | A(B) | B | A |
| (16) Primitive paired lateral gills on abdomen: — A, present on segs. 1–5 or 1–6; B, absent..... | AU | B | B‡ | B‡ | B‡ | B | B‡ |
| Percentage of archaic characters§ for the most archaic members of each family.... | 100 | 75 | 63 | 44 | 56 | 25 | 25 |

*In Perlidæ not as elongated as in Capniidæ and Nemouridæ.

†In Perlidæ, 1 and 2 very short, 3 greatly elongated; in Capniidæ and Nemouridæ, either 1 or 2 elongated.

‡In Leptoperlidæ secondary gills are developed as an anal rosette; in some Pteronarcidæ, Perlidæ and Nemouridæ, secondary gill-tufts are developed in various positions on the thorax or base of abdomen.

§In the table, I have not included the character of the presence or absence of fusion of $M_{3+4}$ with $Cu_1$, or $Cu_{1a}$, in hindwing, as I have been unable to study the tracheation of larval wings in all families. It should be noted that this fusion is absent in Eustheniidæ, but present in both Austroperlidæ and Leptoperlidæ.

KEY TO THE FAMILIES OF THE ORDER PERLARIA.

(1) Anal fan of hindwing well formed, and with a complete archedictyon or original meshwork of cross-veins; the contour of the outer margin of the hindwing a single convex whole, without any re-entrant angle at the end of $Cu_2$.....*Eustheniidæ*, n. fam. (Text Fig. 1).
Anal fan of the hindwing without any archedictyon; outer margin of hindwing with a marked re-entrant angle at end of $Cu_2$.....2.

(2) Anterior coxæ closely approximated; cross-venation retained except on anal fan; mandibles reduced to a weak lamina.....*Pteronarcidæ*.
Anterior coxæ remain widely separated.....3.

(3) Mandibles reduced to a weak lamina; clypeus and labrum become hidden beneath frontal shelf; last joint of tarsi much longer than 1 + 2....*Perlidæ*.
Mandibles, clypeus and labrum remain normal; last joint of tarsi not longer than 1 + 2.....4.

(4) In forewing, three anal veins are present, 1A running very close to $Cu_2$.....*Austroperlidæ*, n. fam. (Text Fig. 3).
In forewing, 1A is eliminated, leaving only 2A and 3A, the latter forked or simple.....5.

(5) In both wings, no true anastomosis connects the main veins from R to $Cu_1$ near middle of wing; cross-veins are always present in the distal portion of the wings.....*Leptoperlidæ*, n. fam. (Text Fig. 4).
A true anastomosis or transverse cord is always present, connecting the main veins of both wings from R to $Cu_1$; cross-veins not usually present distad from the anastomosis.....6.

(6) (In forewing, 3A is forked; cerci are vestigial, being reduced to a single joint.....*Nemouridæ*.
In forewing, 3A is simple; cerci remain long and many-jointed.....*Capniidæ*

FAMILY AUSTROPERLIDÆ.

**Tasmanoperla**, n. g.

(Text Fig. 3).

Allied to *Austroperla* Needham, from which it differs only in the following points:—

Veins of the forewing very strongly marked, cross-venation very prominent, (*Austroperla* has the cross-venation weak, especially in the distal half of the wing, where the cross-veins are not easy to see in most specimens). In the forewing, 1A diverges from $Cu_2$ slightly, then converges towards it distally; (in *Austroperla* 1A lies very close to $Cu_2$ throughout, and is a much more weakly formed vein). Forewing considerably narrowed at the base, without any clearly marked anal angle; (in *Austroperla*, the forewing has a definite anal angle, distad from which the posterior margin runs almost parallel with the costal margin of the wing).

Genotype.—*Eusthenia diversipes*, n. sp. (Tasmania).

## Tasmanoperla diversipes, n. sp.

(Text Fig. 3).

No description of this species appears ever to have been published, although the name is mentioned in literature by Walker and others. It would seem probable that Westwood had made a MS description, from which the name was taken and used in print, without any corresponding description. The species is closely allied to *Eusthenia thalia* Newm., 1839, from which it may be distinguished as follows:—

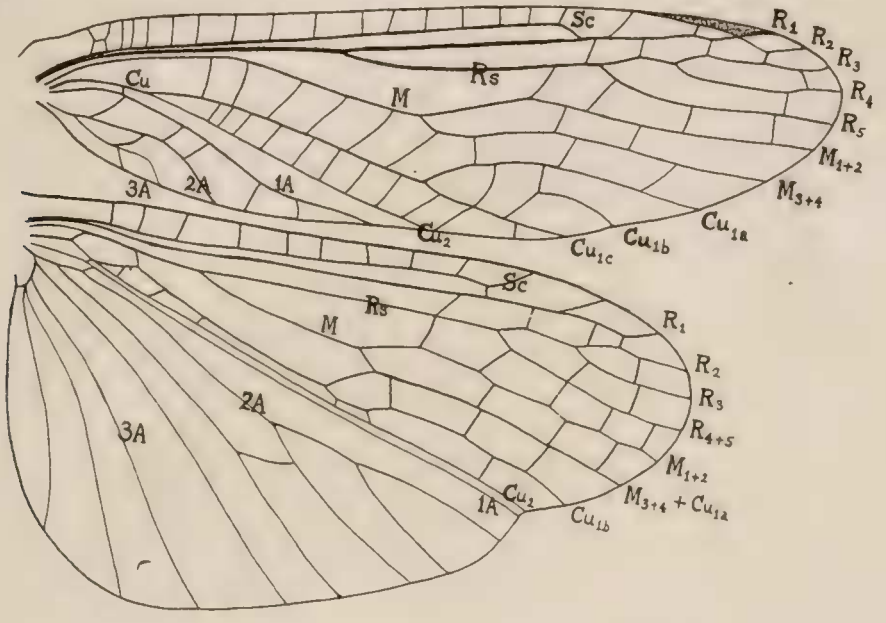


*Fig. 3.*—Venation of *Tasmanoperla diversipes* n. g. et. sp.; family Austroperlidæ.

Wing-veins brown, the costal veinlets of the forewing, and the distal ends of the main veins of both wings around the apices marked with small dark patches. Forewings very irregularly irrorated with brown, but a clear, unshaded patch of irregular shape is left at one-third from apex. (*E. thalia* Newm. has the forewing of a dark smoky colour, with a very clear and more regular, somewhat cream-coloured patch left unshaded in about the same position). Legs black, with rich brown marks at the bases of the femora and tibiæ; the brown on the hind femora occupies the basal half.

As in *E. thalia*, the wings are slightly shorter than the abdomen, the cerci rather short, the antennæ shorter than the forewing, and the prothorax absolutely square in shape.

Type.—Holotype female, in Coll. Tillyard.

Locality.—Mount Wellington, Tasmania, Jan. 31st, 1917.

This species is made the type of the genus *Tasmanoperla* as it is the one which I have studied and figured. I have, however, seen specimens of *E. thalia* Newm., and there can be no doubt that it also must be placed in this genus.

## Family Leptoperlidæ.

### Note on the Type Specimen of Leptoperla Beroe Newm.

(Text Fig. 4a).

The venational characters of *Leptoperla beroë* Newm., which is not only the type of the genus, but also the first Leptoperlid ever described, were not clearly given by Newman. The type is in the Hope Museum, Oxford. By the kindness of Professor Poulton, F. R. S., I was recently able to study this specimen carefully. Text Fig. 4 shows the venation of the right forewing, which has a peculiar aberrancy in that the two branches of M come together and fuse for a short space, and then separate again distally. The left forewing and both hindwings are much rolled and crumpled, the specimen being gummed on card. By softening these wings with warm water, and uncurling them with a fine brush, I was enabled to prove that the left forewing possesses a normal venation, with both branches of M running free and parallel to their tips. The following diagnosis for the genus may now be given:—

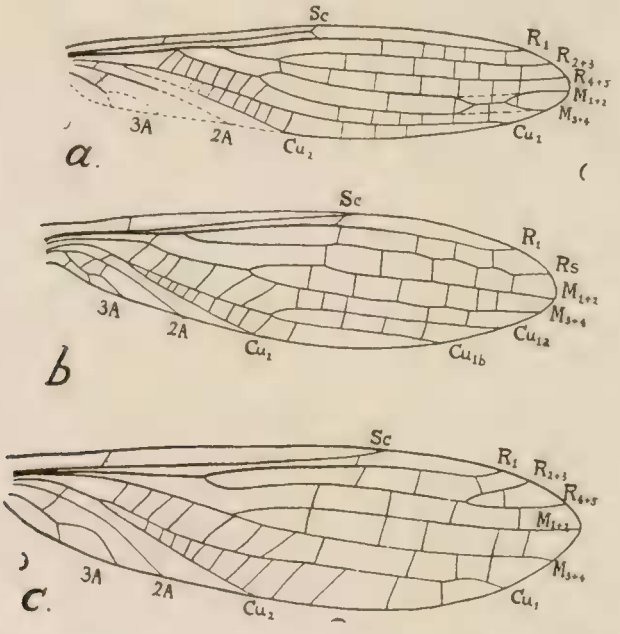


*Fig. 4.*—*A.* Right forewing of type specimen of *Leptoperla beroe* Newm. The normal courses of the branches of M, and the form of the crumpled anal area, as revealed by a study of the damaged left wing, are shown by dotted lines.
*B.* Right forewing of a specimen of *Dinotoperla opposita* (Walk.) from Mount Wellington, Hobart, Tasmania.
*C.* Right forewing of *Zelandobius confusus* (Hare) paratype, from Wellington, New Zealand.

*Antennæ* and *cerci* long, the latter considerably longer than the abdomen. *Forewing* with Sc stopping just short of half-way, its tip forked. Rs and M both forked not far from their origins, $Cu_1$ unforked and very long, running to the same level below the apex of the wing as that at which $R_1$ ends up above it. Complete sets of cross-veins between M and $Cu_1$ and also between $Cu_1$ and $Cu_2$. 2A simple, 3A forked. Irregular cross-veins enclosed in pale, oval spaces occupy positions in the distal half of the wing; (the wing membrane generally is of a brownish colour). *Hindwing* with Sc as in forewing; Rs simple; M with a free upper branch, and with its lower branch fused with $Cu_1$ to the border; $Cu_1$ simple; anal fan with five straight veins excluding 1A. (Cross-veins present

in hindwing are the humeral, an oblique one connecting $R_1$ with Rs towards half-way, and two connecting $Cu_2$ with the fused vein above it in its distal half).

The locality for this species is Tasmania. Though I have collected carefully in many places throughout the island, I have never met with it. The common Leptoperlids of Australia, Tasmania and New Zealand do not belong to this genus.

**Dinotoperla,** n. g.

(Text Fig. 4b).

Cerci shorter than the abdomen. Third joint of tarsus slightly longer than basal joint. Forewings with Rs simple, $Cu_1$ deeply forked, and complete sets of cross-veins between M and $Cu_1$, and also between $Cu_1$ and $Cu_2$. Hindwing with only slight fusion between $M_{3+4}$ and $Cu_1$, and with the anal fan narrower than the rest of the wing at the end of $Cu_2$.

Genotype.—*Leptoperla opposita* Walker, Tasmania.

This genus differs radically from *Leptoperla* Newm. in its much shorter cerci, its longer distal joint of the tarsi, in the loss of the fork of Rs and in the retention of the fork $Cu_1$. It is closely related to *Gripopteryx* End. and *Paragripopteryx* End., from South America (these two genera are barely distinct), but can be at once separated from them by the unforked Rs of the forewing and by the possession of the complete series of cross-veins between M and $Cu_1$.

A number of undescribed species of this genus occur in Australia and Tasmania.

**Zelandobius,** n. g.

(Text Fig. 4c).

Allied to *Gripopteryx* End. and *Paragripopteryx* End. from South America, but distinguished at once from them by possessing a simple $Cu_1$ in forewing and a wide anal fan in the hindwing, as well as by the retention of the complete series of cross-veins between M and $Cu_1$ in forewing. Rs is distally forked as in *Gripopteryx* and *Paragripopteryx*.

Genotype.—*Leptoperla confusa* Hare, New Zealand.

*Leptoperla hudsoni* Hare also goes into this genus, but *L. fulvescens* Hare and *L. maculata* Hare belong to *Aucklandobius* End. All these species are from New Zealand.

*Zelandobius* differs from *Aucklandobius* in having Rs distally forked in the forewing, and the fusion of $M_{3+4}$ with $Cu_1$ not complete in hindwing. *Aucklandobius* differs from *Antarctoperla* End. chiefly in its much wider anal fan and in the complete fusion of $M_{3+4}$ with $Cu_1$ in hindwing.

Both *Zelandobius* and *Aucklandobius* are represented in New Zealand by a number of undescribed species. The *Leptoperlidæ* of South America are evidently closely allied to those of New Zealand and Australia, and a knowledge of all the forms is necessary for the study of those in any one region.

Explanation of Text Figures.

1A, 2A, 3A, first, second and third anal veins, respectively; $Cu_1$, first cubitus, with its branches $Cu_{1a}$, $Cu_{1b}$, $Cu_{1c}$, $Cu_{1d}$; $Cu_2$, second cubitus; $M_{1+2}$, $M_{3+4}$, the two branches of the media; $R_1$, radius; Rs, radial sector, with its branches $R_2$, $R_3$, $R_4$, $R_5$; Sc, subcosta.